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Are There Indirect Fitness Benefits of Female Extra-Pair Reproduction? Lifetime Reproductive Success of Within-Pair and Extra-Pair Offspring

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ABSTRACT: The forces driving extra-pair reproduction by socially monogamous females, and the resulting genetic polyandry, remain unclear. A testable prediction of the hypothesis that extra-pair reproduction partly reflects indirect selection on females is that extra-pair young (EPY) will be fitter than their within-pair young (WPY) maternal half-siblings. This prediction has not been comprehensively tested in a wild population, requiring data on the lifetime reproductive success (LRS) of maternal half-sib EPY and WPY. We used 17 years of genetic parentage data from song sparrows, *Melospiza melodia*, to compare the LRS of hatched EPY and WPY maternal half-siblings measured as their lifetime number of hatched offspring, recruited offspring, and hatched grandoffspring. EPY hatchlings were not significantly fitter than WPY hatchlings for any of three measures of LRS. Furthermore, opposite to prediction, EPY hatchlings tended to have lower LRS than their maternal half-sibling WPY hatchlings on average. EPY also tended to be less likely to survive to hatch than their maternal half-sibling WPY. Taken together, these results fail to support one key hypothesis explaining the evolution of genetic polyandry by socially monogamous females and suggest there may be weak indirect selection against female extra-pair reproduction in song sparrows.

Keywords: extra-pair paternity, fitness, genetic benefits, half-sibling, indirect selection, polyandry.

Introduction

Extra-pair reproduction (EPR), and hence extra-pair paternity (EPP), are widespread in socially monogamous species (Griffith et al. 2002; Sefc et al. 2008; Uller and Olsson 2008; Soulsbury 2010). EPR causes genetic polygynandry and can substantially influence the pattern and magnitude of sexual selection and variation in relatedness and hence shape the evolutionary dynamics of physiology, behavior, and mating systems (Cornell and Tregenza 2007; Webster et al. 2007; Shuster 2009; Cornwallis et al. 2010). However, despite substantial research, the costs and benefits of EPR to males and females, and hence the ecological and evolutionary forces driving this behavior, remain unclear (Griffith et al. 2002; Westneat and Stewart 2003; Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007; Eliassen and Kokko 2008; Uller and Olsson 2008; Slatyer et al. 2011).

One key force driving female EPR is hypothesized to be indirect selection resulting from increased fitness of offspring produced via extra-pair mating (Kempenaers et al. 1997; Sheldon et al. 1997; Griffith et al. 2002). However, evidence supporting the prediction that extra-pair young (EPY) will be fitter than their maternal half-sib within-pair young (WPY) remains scarce (Griffith et al. 2002; Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007; Schmoll et al. 2009). Testing this prediction, and hence demonstrating indirect selection on female EPR, therefore remains a key aim in evolutionary ecology (Kempenaers 2007; Hasson and Stone 2011; Schmoll 2011; Slatyer et al. 2011).

The widespread occurrence of EPR and mixed paternity broods (with ≥1 EPY and ≥1 WPY) in socially monogamous birds provides an empirically tractable opportunity to test the prediction that extra-pair young (EPY) sired by extra-pair males will be fitter than their within-pair young (WPY) maternal half-siblings sired by a female's social mate (Kempenaers et al. 1997; Sheldon et al. 1997; Griffith et al. 2002; Schmoll et al. 2009; Hasson and Stone 2011). Higher fitness of EPY than their same-brood maternal half-sib WPY may reflect genetic effects of the extra-pair

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sire since other sources of variation in fitness, such as average effects of maternal genes and brood environment, should be similar across maternal half-siblings (Kempenaers et al. 1997; Sheldon et al. 1997; Griffith et al. 2002; but see "Discussion").

Rigorous test of this prediction requires a comparison of the lifetime fitness of maternal half-sib EPY and WPY (Eliassen and Kokko 2008; Schmoll et al. 2009; Hasson and Stone 2011). Fitness is difficult to measure in the wild but can be approximated as the lifetime number of offspring produced at various life-history stages (lifetime reproductive success [LRS]; Brommer et al. 2002; Hunt et al. 2004). For example, LRS is often measured as the lifetime number of offspring that survive to the earliest life-history stage at which parentage can be assigned, commonly soon after hatch or birth ($LRS_{hatched}$; e.g., Wilson et al. 2005; Schmoll et al. 2009; Blomquist 2010). However, if offspring quantity and survival are negatively related, the number of offspring that survive to breed may represent lifetime fitness more closely than the number initially produced (Brommer et al. 2004; Gillespie et al. 2008). LRS measured as the lifetime number of offspring that recruit to the breeding population may thus be more informative ($LRS_{recruited}$; e.g., Jensen et al. 2004; MacColl and Hatchwell 2004; Rödel et al. 2009) but still does not capture variation in fitness due to an offspring's own reproductive success. Measuring the lifetime number of grandoffspring, however, accounts for both of these caveats (LRS_{grand}; e.g., MacColl and Hatchwell 2004; Gillespie et al. 2008; Dugdale et al. 2010). Moreover, the success of second-generation descendants may be particularly relevant in the context of quantifying selection on reproductive behavior since the fitness benefits to a focal individual may be manifested as increased reproductive success of offspring (Brommer et al. 2004; Hunt et al. 2004; Gillespie et al. 2008).

There are advantages and disadvantages to all measures of LRS. Counting hatched offspring fails to capture variation in offspring survival and reproductive success and hence long-term fitness, whereas counting recruited offspring or grandoffspring confounds parent and offspring fitness (Wolf and Wade 2001; Hunt et al. 2004; Wilson et al. 2005). Furthermore, dispersal, which often occurs before recruitment, may introduce error and/or bias in LRS measured as recruited offspring or grandoffspring relative to the number of locally hatched offspring (Lambrechts et al. 1999; Brommer et al. 2004; MacColl and Hatchwell 2004). For these reasons we tested the prediction that EPY are fitter than their WPY maternal half-sibs by comparing LRS at multiple life-history stages.

Estimating LRS in populations where EPR occurs requires genetic parentage to be accurately assigned to all offspring produced across multiple generations, but this is rarely achieved in wild populations (Sardell et al. 2010). Consequently, most studies that have tested for indirect benefits of EPR have compared EPY and WPY half-siblings with respect to nestling or juvenile traits that are hypothesized to indicate fitness, such as morphology, condition, immunocompetence, or early survival (e.g., Sheldon et al. 1997; Johnsen et al. 2000; Whittingham and Dunn 2001; Akçay and Roughgarden 2007; Suter et al. 2007). A few studies have compared survival to adulthood or lifespan (Kempenaers et al. 1997; Charmantier et al. 2004; Grant and Grant 2011; Sardell et al. 2011). One notable study compared LRS, but with male reproductive success measured as the number of offspring reared rather than sired (Schmoll et al. 2009). However, if there are trade-offs among life-history components, comparing juvenile traits or survival between EPY and WPY may provide misleading evidence regarding the difference in lifetime fitness. Since the fitness benefit of polyandry could be manifested as increased mating success of a female's sons (Pai and Yan 2002; Kokko et al. 2003; Head et al. 2005; Evans and Simmons 2008; Klemme et al. 2008; Firman 2011), which may not be mirrored by increased fitness of daughters (Brommer et al. 2007; Sardell et al. 2011), the ultimate requirement is to quantify the difference in LRS among male and female EPY and WPY measured from conception.

A further practical difficulty in achieving this aim is that offspring can usually only be assigned to genetic parents postconception. Some studies have compared the early survival of EPY and WPY to hatch or birth (Whittingham and Dunn 2001; Bouwman et al. 2007; Suter et al. 2007), which may be key if early mortality varies with paternity (Simmons 2005; Griffith and Immler 2009). However, a comprehensive test of the prediction that EPY are fitter than their WPY maternal half-sibs and hence that polyandry is under indirect selection requires the fitness of EPY and WPY to be measured across all life-history stages in the same population; this has not been achieved.

We used 17 years of genetic parentage data from an intensively studied song sparrow, *Melospiza melodia*, population where individual LRS can be measured with unusual precision, to compare the lifetime number of hatched offspring ($LRS_{hatched}$), recruited offspring ($LRS_{recruited}$), and hatched grandoffspring (LRS_{grand}) produced by male and female maternal half-sibling EPY and WPY hatchlings and recruits. Because these main analyses included only half-siblings that survived to posthatch paternity assignment, they exclude any prior difference in survival of WPY versus EPY. We therefore also compared the probability of survival to hatch between EPY and WPY maternal half-sibs across broods in which unhatched offspring could be assigned to sires. We thereby test the prediction that EPY are fitter than their maternal half-sib WPY and discuss the

implications for the hypothesis that female EPR is under indirect selection through increased fitness of EPY.

Methods

Study System

A small, resident population of socially monogamous song sparrows (numbering 33–131 adults during 1993–2010) inhabiting Mandarte Island, British Columbia, Canada, has been studied intensively since 1975 (Smith et al. 2006). All song sparrows present on Mandarte have been color-ringed as hatchlings or newly arrived immigrants, meaning that all individuals are identifiable by resighting. Both sexes regularly breed at age 1 year. Females typically rear two broods per year (range 1–4) with median clutch size 4 eggs (range 1–5; Smith et al. 2006). All territories were visited at least weekly during April–July to find all nests and identify all social parents (those defending territories, incubating clutches, and provisioning hatchlings). All nests were visited ~6 days posthatch, when all hatchlings were color-ringed and bled. Juveniles and adults surviving to subsequent breeding seasons were resighted with probability ≈ 1 (Wilson et al. 2007). Despite several other islands nearby, immigration is infrequent (~1.1 immigrants per year) but sufficient to maintain neutral allelic diversity (Keller et al. 2001). Local recruitment rate is high compared to other populations of song sparrows and species with similar life histories (Sardell et al. 2011). Searches of nearby islands have revealed few juvenile emigrants, and no adult breeders on Mandarte have been observed breeding elsewhere (Smith et al. 2006; Sardell et al. 2011). Juvenile emigration is therefore limited, and postrecruitment emigration is extremely rare.

Paternity Assignment and Molecular Sexing

Each year during 1993–2009, a small blood sample was collected from virtually all (99.4%) 6-day-old hatchlings ($N = 2{,}343$ hatchlings from 854 broods), all adult immigrants to Mandarte and most adults alive in 1993 (Sardell et al. 2010). Eggs and hatchlings that disappeared before 6 days posthatch due to brood reduction or complete nest failure were not sampled. Any unhatched eggs that remained in nests were checked for development and unhatched offspring collected where possible (Taylor et al. 2010). Virtually all hatchlings and collected unhatched offspring were genotyped at 13 microsatellite loci and assigned sires using Bayesian full probability models that incorporated both genetic and spatial information (Sardell et al. 2010). Sires were assigned to 99.1% (2,322/2,343) and 99.7% (2,335/2,343) hatchlings with ≥95% and ≥80% individual-level confidence, respectively. All 57 collected unhatched offspring were assigned sires with ≥85% individual-level confidence. Virtually all offspring were therefore assigned as either WPY (sired by the male defending the female's territory during egg-laying) or EPY (sired by a different male) with high statistical confidence (Sardell et al. 2010). The maximum likelihood probability of correctly excluding a female's social mate as sire was 0.9998. The EPP rate over 17 years was ~28% (Sardell et al. 2010), similar to a nearby mainland population (24%; Hill et al. 2011) and to many other bird species (Griffith et al. 2002). All hatched offspring were sexed using the CHD-1 gene (Postma et al. 2011). Molecular sexes were 100% consistent with those attributed from behavioral observations for all recruited individuals.

Fitness of EPY versus WPY

Generalized linear mixed models (GLMMs) were used to estimate the relative $LRS_{hatched}$, $LRS_{recruited}$, and LRS_{grand} of maternal half-sib EPY and WPY. Two analyses were run for each of the three measures of LRS. The first analysis compared the LRS of a female's EPY hatchlings with her WPY hatchlings and therefore included hatchlings that died before recruitment. The second analysis compared the LRS of recruited EPY with recruited WPY and therefore excluded EPY and WPY that died before recruitment. This second analysis allowed the LRS of male EPY and WPY recruits to be explicitly compared, one key fitness component that previous studies have not measured (Schmoll et al. 2009). Importantly, comparison of $LRS_{hatched}$ between recruited EPY and WPY also provides the only fitness comparison that cannot be biased by any juvenile emigration.

All analyses were restricted to maternal half-siblings from known mixed paternity broods (containing ≥1 WPY and ≥1 EPY) at hatching in case the occurrence of EPP covaried with maternal or environmental variation in fitness which could potentially bias among-brood comparisons (Sheldon et al. 1997; Magrath et al. 2009; Schmoll et al. 2009). Although there were few broods from which ≥1 EPY and ≥1 WPY recruited, analyses of recruit LRS were also restricted to individuals from broods of known mixed paternity at hatching to minimize any bias due to environment or maternal variation. Analyses were further restricted to hatchlings from the 1993–2003 cohorts since no individuals were still alive in 2010. The $LRS_{hatched}$ and $LRS_{recruited}$ could therefore be measured for all individuals. However, seven individuals hatched during 1993–2003 had some offspring (≤2 offspring of age ≥3 years) still alive in 2010. The LRS_{grand} for these seven individuals was therefore incompletely estimated. These seven individuals were retained in analyses because excluding them would bias the data set toward short-lived lineages with low LRS_{grand}. Since

reproductive success tends to decrease beyond age 3 years in song sparrows (Smith et al. 2006; Keller et al. 2008), LRS_{grand} for these seven individuals is unlikely to be substantially underestimated. Moreover, since all seven had ≥1 grandoffspring, they did not introduce any error into analyses that estimated the probability that $LRS_{grand} \geq 1$ (see below).

All analyses included fixed effects of an individual's extra-pair status (EPY or WPY), natal season (whether an individual hatched in an early or late season brood; Sardell et al. 2011), and sex. LRS differs between recruited males and females in the study population because the adult sex ratio is typically male biased (Smith et al. 2006). All analyses also included random effects of an individual's natal brood nested within social parent pair, thereby accounting for variation among broods raised by the same and different pairs. Random cohort effects were also included in all models to account for known among-cohort variation in LRS (Smith et al. 2006). An extra-pair status by sex interaction was then modeled to test whether effects of extra-pair status on LRS varied with offspring sex (Sardell et al. 2011). Extra-pair status by natal season interactions were also initially modeled but were never significant and are not reported. Although the total sample size of hatchlings whose LRS was measured was large, the number per cohort was relatively small (table A1, available online). Therefore, we did not test whether any difference in LRS between EPY and WPY varied among cohorts. The magnitude and statistical significance of main fixed effects were estimated from models without interactions. All fixed effects were retained in all main models (even if not statistically significant across the current restricted data set) due to a priori knowledge of their effects on LRS. However, all analyses were also rerun with extra-pair status as the only fixed effect to directly estimate the mean difference in LRS between EPY and WPY across offspring of both sexes and natal seasons and hence the overall benefit or cost of EPR to a polyandrous female.

Inbreeding coefficient (f) has sex-specific effects on LRS in Mandarte's song sparrows (Keller et al. 2008). However, f was not included in current analyses because EPY and WPY may differ in f if EPR permits inbreeding avoidance. Controlling for f may therefore control for part of the variation that our current aim is to measure. However, in practice, conclusions remained quantitatively similar when analyses were rerun including a regression on f and sex by f interaction.

Hatched versus Unhatched Offspring

The above analyses excluded individuals that died before standard paternity assignment at 6 days posthatch. We therefore used the available sample of unhatched offspring and their hatched maternal half-sibs to test whether the probability of survival to hatch differed between EPY and WPY. This analysis used 23 mixed paternity broods containing ≥1 hatchling and ≥1 unhatched offspring in a GLMM with extra-pair status as the sole fixed effect and random effects of brood and cohort. As sexes of some unhatched offspring could not be ascertained due to poor DNA quality, effects of sex, and sex by extra-pair status interaction were not modeled. However, as the sex ratio at 6 days posthatch was close to 50 : 50, there was unlikely to be any sex bias in survival to this stage (Postma et al. 2011).

Model Fitting

Distributions of $LRS_{hatched}$, $LRS_{recruited}$, and LRS_{grand} for hatchlings were substantially overdispersed and zero-inflated relative to Poisson as most hatchlings had zero LRS. Initial models for hatchling LRS specified Poisson distributions with additive overdispersion, but the residual variance remained large. Final models therefore specified zero-altered Poisson (zapoisson) distributions, which comprise a zero-truncated Poisson process (estimating the number of offspring given that $LRS \geq 1$ using a log link function) and a zero-altered binomial process (estimating the probability that $LRS \geq 1$ using a complementary log-log link function). The probability that $LRS \geq 1$ was also estimated with LRS specified as a binary trait, with binomial errors and logit link function. These analyses gave quantitatively similar results to those from the zero-altered process in the zapoisson models (see app. A, available online).

Distributions of $LRS_{hatched}$ and $LRS_{recruited}$ for recruited EPY and WPY were overdispersed relative to Poisson but not sufficiently zero-inflated to justify fitting zapoisson models. Two sets of models were therefore run; one estimating the number of offspring produced (specifying a Poisson distribution with log link function and additive overdispersion) and one estimating the probability that $LRS \geq 1$ (specifying a binary distribution with logit link function). The binary model did not converge for $LRS_{hatched}$ when sex was included in the model because female recruits virtually always had $LRS_{hatched} \geq 1$. The distribution of LRS_{grand} for recruits was overdispersed and zero-inflated relative to Poisson. Models therefore specified a zapoisson distribution, and data were reanalyzed specifying a binary distribution for the probability that $LRS_{grand} \geq 1$ (see app. A). Analysis of survival to hatch specified a binary distribution with logit link.

GLMMs were fitted using Bayesian Markov Chain Monte Carlo (MCMC) methods using the R package MCMCglmm, version 2.09, in R, version 2.10.0, to allow the required effects and associated uncertainty to be ro-

bustly estimated (R Development Core Team 2009; Hadfield 2010). For binary models, the residual variance cannot be estimated and was fixed to 1 by convention. Priors on fixed effects were normally distributed, diffuse, and proper, with mean zero and large variance (10^8). Zapoisson models used parameter-expanded priors on variance components with a mean (alpha.mu) of 0 and large variance (alpha.V) of 1,000 to facilitate mixing (Hadfield 2010). Inverse-Wishart distributed priors with variance 1 and degree of belief 0.002 were used on variance components in Poisson and binary models. Prior sensitivity analysis and binary models fitted using maximum likelihood showed that estimates were robust to reasonable variation in prior specifications and fitting methods. MCMC models used burn-in 50,000, 10,050,000 iterations, and thinning interval 1,000 to give an effective sample size of 10,000. Autocorrelation among consecutive samples was low (<0.05). MCMC *P* values and 95% credible intervals (95% CIs) surrounding posterior means were used to assess statistical significance. To aid visualization of biological effects, posterior means and 95% CIs estimated on transformed scales were back transformed onto observed data scales. Back-transformed estimates from zapoisson models gave the predicted mean LRS given that LRS $\geq$ 1 and the probability that LRS $\geq$ 1. Effects estimated from zapoisson models could not be marginalized across random effects because the necessary transformations have not been developed. Back-transformed estimates and CIs from zapoisson models therefore do not account for random effects but are presented to facilitate interpretation. Raw data describing the proportions of EPY and WPY for which $LRS_{hatched}$, $LRS_{recruited}$, and $LRS_{grand} \geq 1$, and the median, mean, and range of these fitness measures are provided in table A3, available online.

Results

Distributions of LRS

Across the total of 471 hatchlings representing 154 mixed paternity broods and 117 social parent pairings, only 16.6%, 11.9%, and 10.6% of hatchlings had $LRS_{hatched}$, $LRS_{recruited}$, and $LRS_{grand} \geq 1$, while the maximum values were 50, 18, and 192, respectively (table A3).

Across the total of 99 recruits representing 77 mixed paternity broods and 65 social parent pairings 78.8%, 56.6%, and 50.5% of recruits had $LRS_{hatched}$, $LRS_{recruited}$, and $LRS_{grand} \geq 1$, respectively (table A3).

$LRS_{hatched}$ for Hatchlings

In the full zapoisson GLMM fitted to $LRS_{hatched}$ for all 471 hatchlings no fixed effects were statistically significant (table 1). However, back-transformed estimates showed that female EPY had 5.4 fewer hatched offspring than female WPY on average, while male EPY had 1.5 fewer hatched offspring than male WPY (fig. 1*A*). Female EPY were 6% less likely to have ≥1 hatched offspring than female WPY, while male EPY were 2% more likely to have ≥1 hatched offspring than male WPY (fig. 1*D*). When the zapoisson model was rerun with extra-pair status as the only fixed effect, extra-pair status had a statistically significant effect on the zero-truncated Poisson process but not on the zero-altered process (table 1); EPY had 3.6 fewer hatched offspring than WPY on average, and were 1% less likely to have ≥1 hatched offspring (fig. 2*A*, 2*D*).

$LRS_{hatched}$ for Recruits

In the Poisson GLMM fitted to $LRS_{hatched}$ for all 99 recruits, the effect of sex was statistically significant; male recruits had lower $LRS_{hatched}$ than female recruits (table 2). Other fixed effects were not statistically significant (table 2). However, back-transformed estimates showed that female EPY recruits had 6.4 fewer hatched offspring than female WPY recruits on average, while male EPY recruits had 2.6 fewer hatched offspring than male WPY recruits (fig. 3*A*). When the Poisson model was rerun with extra-pair status as the only fixed effect, extra-pair status was again not statistically significant. However, EPY recruits had 6.6 fewer hatched offspring than WPY recruits on average (table 2; fig. 4*A*). When the binary model was run with extra-pair status as the only fixed effect, extra-pair status was not statistically significant, but EPY were 9% less likely to have ≥1 hatched offspring than WPY (table 2; fig. 4*D*).

$LRS_{recruited}$ for Hatchlings

In the full zapoisson GLMM fitted to $LRS_{recruited}$ for all 471 hatchlings, no fixed effects were statistically significant (table 1). Estimated effects were also small; back-transformed estimates showed that female EPY had 0.2 more recruited offspring than female WPY on average, while male EPY had 0.2 fewer recruited offspring than male WPY (fig. 1*B*). Female EPY were 6% less likely to have ≥1 recruited offspring than female WPY, while male EPY were 1% more likely to have ≥1 recruited offspring than male WPY (fig. 1*E*). When the zapoisson model was rerun with extra-pair status as the only fixed effect, extra-pair status was again not statistically significant; EPY had 0.1 more recruited offspring than WPY on average but were 2% less likely to have ≥1 recruited offspring (table 1; fig. 2*B*, 2*E*).

Table 1: Zero-altered Poisson GLMMs explaining variation in lifetime reproductive success (LRS)

	Intercept		Extra-pair status		Sex		Season		Extra-pair status × sex	
Model, parameter	P	ZA	P	ZA	P	ZA	P	ZA	P	ZA
A:										
(i):										
Mean	**2.19**	**−4.27**	**−.51**	.38	...	...	...	...	...	...
95% CI	**1.83, 2.55**	**−5.04, −3.53**	**−.97, −.05**	−.28, 1.10	...	...	...	...	...	...
MCMC *P*	**<.01**	**<.01**	**.03**	.27	...	...	...	...	...	...
(ii):										
Mean	**2.30**	**−4.24**	−.45	.31	−.32	.37	.04	−.47	.43	.22
95% CI	**1.84, 2.76**	**−5.14, −3.40**	−.93, .03	−.40, 1.00	−.82, .18	−.33, 1.12	−.45, .58	−1.24, .29	−.61, 1.45	−1.24, 1.69
MCMC *P*	**<.01**	**<.01**	.06	.38	.21	.30	.87	.23	.40	.78
B:										
(i):										
Mean	.37	**−2.82**	.04	−.35	...	...	...	...	...	...
95% CI	−.30, .99	**−3.78, −1.88**	−.68, .80	−1.30, .62	...	...	...	...	...	...
MCMC *P*	.26	**<.01**	.91	.46	...	...	...	...	...	...
(ii):										
Mean	.56	**−2.72**	−.01	−.32	−.09	−.19	−.55	.05	−.18	1.11
95% CI	−.25, 1.36	**−3.87, −1.65**	−.83, .80	−1.35, .70	−1.01, .79	−1.30, .90	−1.46, .39	−1.09, 1.19	−2.01, 1.53	−1.06, 3.32
MCMC *P*	.16	**<.01**	.99	.54	.84	.72	.24	.94	.84	.31
C:										
(i):										
Mean	**3.13**	**−5.74**	−.37	.01	...	...	...	...	...	...
95% CI	**2.61, 3.68**	**−6.70, −4.80**	−.99, .27	−.86, .93	...	...	...	...	...	...
MCMC *P*	**<.01**	**<.01**	.24	.98	...	...	...	...	...	...
(ii):										
Mean	**3.10**	**−5.31**	−.46	.11	.30	−.71	−.20	−.40	.35	.66
95% CI	**2.46, 3.73**	**−6.36, −4.26**	−1.15, .22	−.83, 1.03	−.46, 1.10	−1.74, .27	−.97, .55	−1.39, .71	−1.12, 1.81	−1.32, 2.62
MCMC *P*	**<.01**	**<.01**	.18	.82	.44	.16	.61	.45	.63	.51
D:										
(i):										
Mean	**3.12**	**−3.31**	−.37	−.41	...	...	...	...	...	...
95% CI	**2.60, 3.69**	**−4.48, −2.03**	−1.00, .28	−1.97, 1.08	...	...	...	...	...	...
MCMC *P*	**<.01**	**<.01**	.24	.63	...	...	...	...	...	...
(ii):										
Mean	**3.09**	**−2.27**	−.46	.09	.30	**−1.93**	−.20	−.40	.34	.21
95% CI	**2.45, 3.77**	**−3.70, −.76**	−1.16, .25	−1.35, 1.52	−.44, 1.10	**−3.42, −.53**	−1.01, .56	−1.98, 1.19	−1.11, 1.91	−2.88, 3.22
MCMC *P*	**<.01**	**.02**	.19	.86	.44	**<.01**	.62	.61	.65	.89

Note: Zero-altered Poisson GLMMs explaining variation in the lifetime number of hatched offspring ($LRS_{hatched}$ [LRS = lifetime reproductive success]; A), recruited offspring ($LRS_{recruited}$; B), and hatched grandoffspring (LRS_{grand}; C) for 471 hatchlings and hatched grandoffspring (LRS_{grand}; D) for 99 recruits from mixed paternity broods. Mean estimates for the zero-truncated Poisson (P) and zero-altered (ZA) processes are presented for each fixed effect (with 95% credible intervals [95% CI] and MCMC *P* values). Mean ZA estimates are expressed as contrasts from Poisson estimates. Each model was run with fixed effects of extra-pair status only (i), and extra-pair status, sex, and season (ii). Estimates for the extra-pair status by sex interaction are from models including this term; all other estimates are from models excluding this term. The intercept corresponds to within-pair young (i) or female within-pair young from early season broods. Bold indicates statistically significant effects (ii).

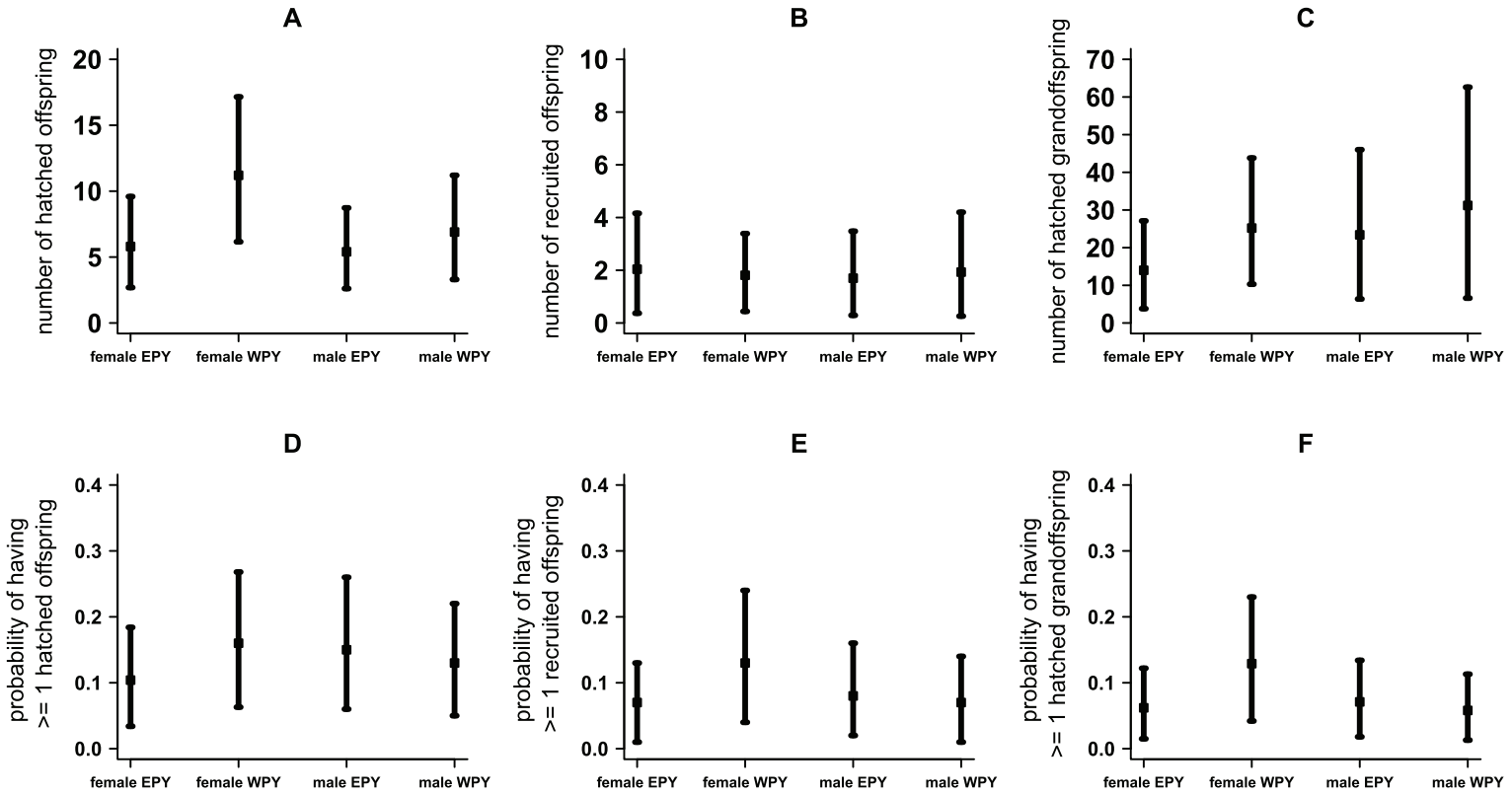

Figure 1: Back-transformed estimates (with 95% credible intervals) from zero-altered Poisson GLMMs for the lifetime number of hatched offspring ($LRS_{hatched}$ [LRS = lifetime reproductive success]; *A*), recruited offspring ($LRS_{recruited}$; *B*), and hatched grandoffspring (LRS_{grand}; *C*); and probability of having ≥1 hatched offspring (*D*), recruited offspring (*E*), and hatched grandoffspring (*F*) for 471 male and female extra-pair young (EPY) and within-pair young (WPY) hatchlings. Estimates for *A*, *B*, and *C* are from the zero-truncated Poisson process and therefore estimate LRS given that LRS ≥ 1.

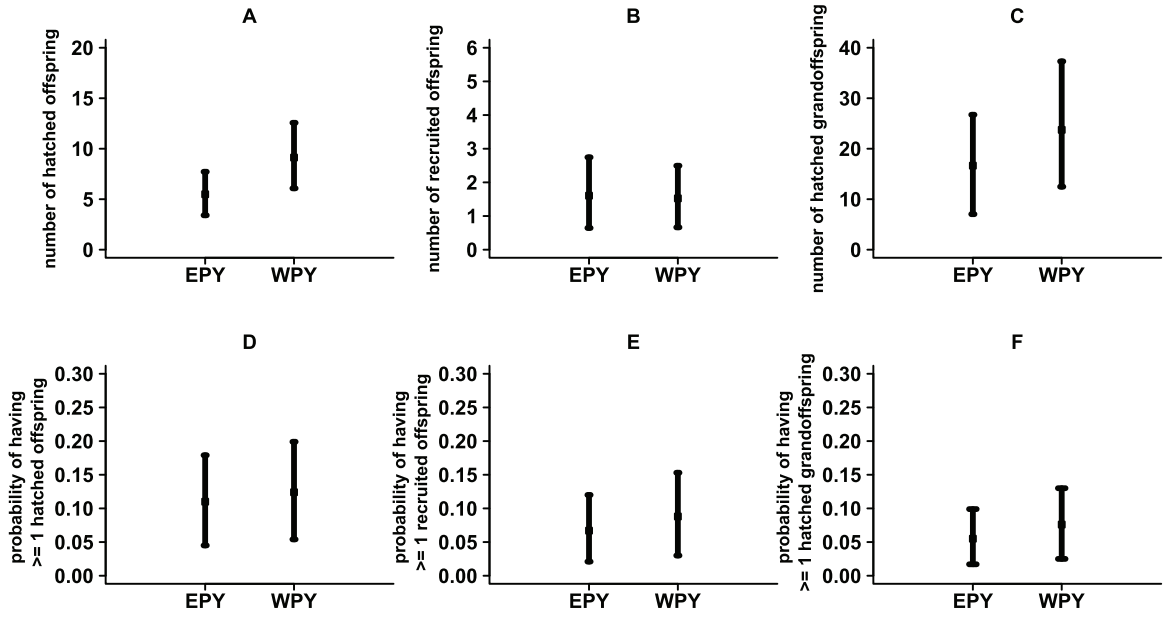

Figure 2: Back-transformed estimates (with 95% credible intervals) from zero-altered Poisson GLMMs for the lifetime number of hatched offspring ($LRS_{hatched}$ [LRS = lifetime reproductive success]; *A*), recruited offspring ($LRS_{recruited}$; *B*), and hatched grandoffspring (LRS_{grand}; *C*); and the probability of having ≥1 hatched offspring (*D*), recruited offspring (*E*), and hatched grandoffspring (*F*) for 471 extra-pair young (EPY) and within-pair young (WPY) hatchlings. Estimates are from models that included a fixed effect of extra-pair status only. Estimates for *A*, *B*, and *C* are from the zero-truncated Poisson process and therefore estimate LRS given that LRS ≥ 1.

$LRS_{recruited}$ for Recruits

In the Poisson GLMM fitted to $LRS_{recruited}$ for the 99 recruits, the effect of sex was statistically significant; male recruits had fewer recruited offspring than female recruits (table 2). The other fixed effects were not statistically significant (table 2). Indeed, back-transformed estimates showed that female EPY and WPY recruits had similar numbers of recruited offspring on average, while male EPY recruits had 0.1 fewer recruited offspring than male WPY recruits (fig. 3*B*). The binary GLMM also showed a statistically significant effect of sex (males were less likely to have ≥1 recruited offspring than females), but other fixed effects again were not statistically significant (table 2). Female EPY recruits were 6% less likely to have ≥1 recruited offspring than female WPY recruits on average, and male EPY recruits were 2% less likely to have ≥1 recruited offspring than male WPY recruits (fig. 3*D*). When these models were rerun with extra-pair status as the only fixed effect, extra-pair status was not statistically significant in either case; EPY recruits had 0.3 fewer recruited offspring than WPY recruits on average, and EPY recruits were 8% less likely to have ≥1 recruited offspring than WPY recruits (table 2; fig. 4*B*, 4*E*).

LRS_{grand} for Hatchlings

In the full zapoisson GLMM fitted to LRS_{grand} for all 471 hatchlings, no fixed effects were statistically significant (table 1). However back transformation showed that the estimated effects were substantial; female EPY had 11.2 fewer grandoffspring than female WPY on average, while male EPY had 7.8 fewer grandoffspring than male WPY (fig. 1*C*). Female EPY were 7% less likely to have ≥1 grandoffspring than female WPY, while male EPY were 1% more likely to have ≥1 grandoffspring than male WPY (fig. 1*F*). When the zapoisson model was rerun with extra-pair status as the only fixed effect, extra-pair status was not statistically significant (table 1). However, EPY had 7.1 fewer grandoffspring than WPY on average and were 2% less likely to have ≥1 grandoffspring (fig. 2*C*, 2*F*).

LRS_{grand} for Recruits

In the zapoisson GLMM fitted to LRS_{grand} for the 99 recruits sex had a statistically significant effect on the zero-altered process but not the zero-truncated process; males were less likely to have ≥1 grandoffspring than females (table 1). The other fixed effects were not statistically sig-

Table 2: GLMMs explaining variation in recruit lifetime reproductive success (LRS)

Model, parameter	Intercept	Extra-pair status	Sex	Season	Extra-pair status × sex
A:					
(i):					
Mean	**.58**	−.46	...	...	...
95% CI	**−.26, 1.43**	−1.52, .65	...	...	...
MCMC *P*	**.16**	.39	...	...	...
B:					
(i):					
Mean	**1.59**	−.51	...	...	...
95% CI	**1.10, 2.11**	−1.09, .12	...	...	...
MCMC *P*	**<.01**	.10	...	...	...
(ii):					
Mean	**2.10**	−.33	**−.89**	−.16	.06
95% CI	**1.51, 2.67**	−.96, .56	**−1.51, −.27**	−.77, .50	−1.27, 1.29
MCMC *P*	**<.01**	.29	**<.01**	.62	.91
C:					
(i):					
Mean	−.12	−.17	...	...	...
95% CI	−.76, .45	−.81, .43	...	...	...
MCMC *P*	.69	.59	...	...	...
(ii):					
Mean	**1.78**	−.22	**−1.81**	−.49	.34
95% CI	**.57, 2.98**	−1.42, .91	**−3.04, −.63**	−1.63, .67	−2.12, 2.82
MCMC *P*	**<.01**	.70	**<.01**	.41	.78
D:					
(i):					
Mean	.71	−.54	...	...	...
95% CI	−.47, 2.05	−1.91, .78	...	...	...
MCMC *P*	.21	.42	...	...	...
(ii):					
Mean	.45	−.05	**−.77**	−.45	−.02
95% CI	−.16, 1.10	−.68, .58	**−1.42, −.09**	−1.09, .23	−1.29, 1.31
MCMC *P*	.16	.88	**.02**	.18	.97

Note: GLMMs explaining variation in measures of lifetime reproductive success for 99 recruits from mixed paternity broods; probability of having ≥1 hatched offspring (A), lifetime number of hatched offspring ($LRS_{hatched}$; B), probability of having ≥1 recruited offspring (C), and lifetime number of recruited offspring ($LRS_{recruited}$, D). Mean estimates for each fixed effect are presented (with 95% credible intervals [95% CI] and MCMC *P* values). Each model was run with fixed effects of extra-pair status only (i) and extra-pair status, sex, and season (ii). A model for the probability of having ≥1 hatched offspring did not converge when sex was included because virtually all female recruits had ≥1 hatched offspring. Estimates for the extra-pair status by sex interaction are from models including this term; all other estimates are from models excluding this term. The intercept corresponds to within-pair young (i) and female within-pair young from early season broods (ii). Bold indicates statistically significant effects.

nificant (table 1). However back-transformed estimates were again substantial; female EPY recruits had 11.0 fewer grandoffspring than female WPY recruits on average, while male EPY recruits had 7.8 fewer grandoffspring than male WPY recruits (fig. 3*C*). Female EPY recruits were 16% less likely to have ≥1 grandoffspring than female WPY recruits, while male EPY recruits were 2% less likely to have ≥1 grandoffspring than male WPY recruits (fig. 3*E*). When the zapoisson model was rerun with extra-pair status as the only fixed effect, extra-pair status was not statistically significant, but EPY recruits had 7.2 fewer grandoffspring than WPY recruits on average and were 22% less likely to have ≥1 grandoffspring (table 1; fig. 4*C*, 4*F*).

Survival to Hatch

The 23 mixed paternity broods used to estimate the effect of extra-pair status on offspring survival to hatch comprised 27 unhatched offspring of which 67% (18/27) were EPY and 44 hatched offspring of which 45% (20/44) were EPY. The probability of survival to hatch was marginally significantly different between EPY and WPY (posterior

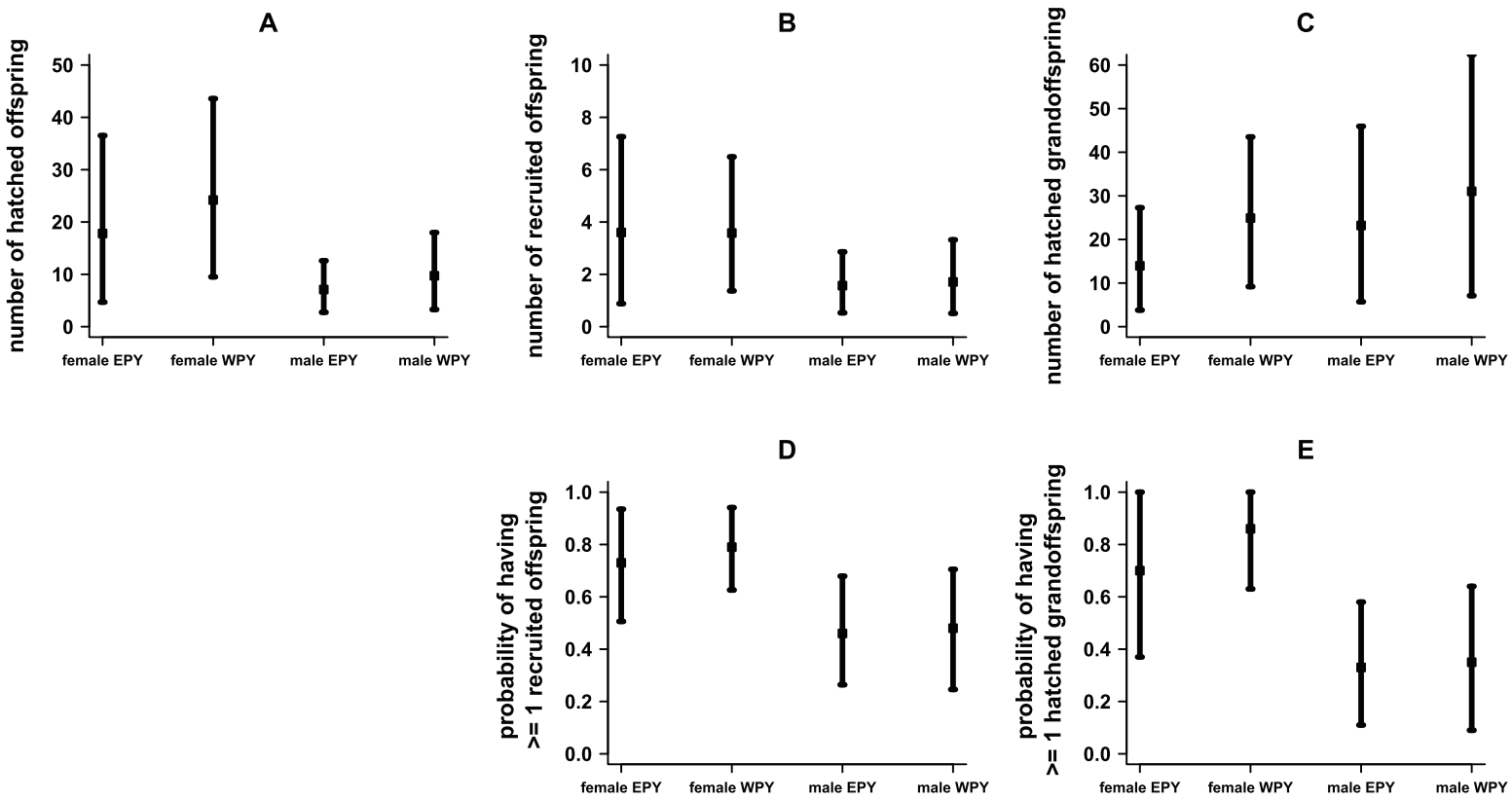

Figure 3: Back-transformed estimates (with 95% credible intervals) of the lifetime number of hatched offspring ($LRS_{hatched}$ [LRS = lifetime reproductive success], Poisson model; *A*), recruited offspring ($LRS_{recruited}$, Poisson model; *B*), and hatched grandoffspring (LRS_{grand}, zero-altered Poisson model; *C*); and the probability of having ≥1 recruited offspring (binary model; *D*) and hatched grandoffspring (zero-altered Poisson model; *E*) for 99 recruited male and female extra-pair young (EPY) and within-pair young (WPY). The binary model for $LRS_{hatched}$ did not converge because virtually all female recruits had ≥1 hatched offspring. Estimates for *C* are from the zero-truncated Poisson process and therefore estimate LRS_{grand} given that $LRS_{grand} \geq 1$.

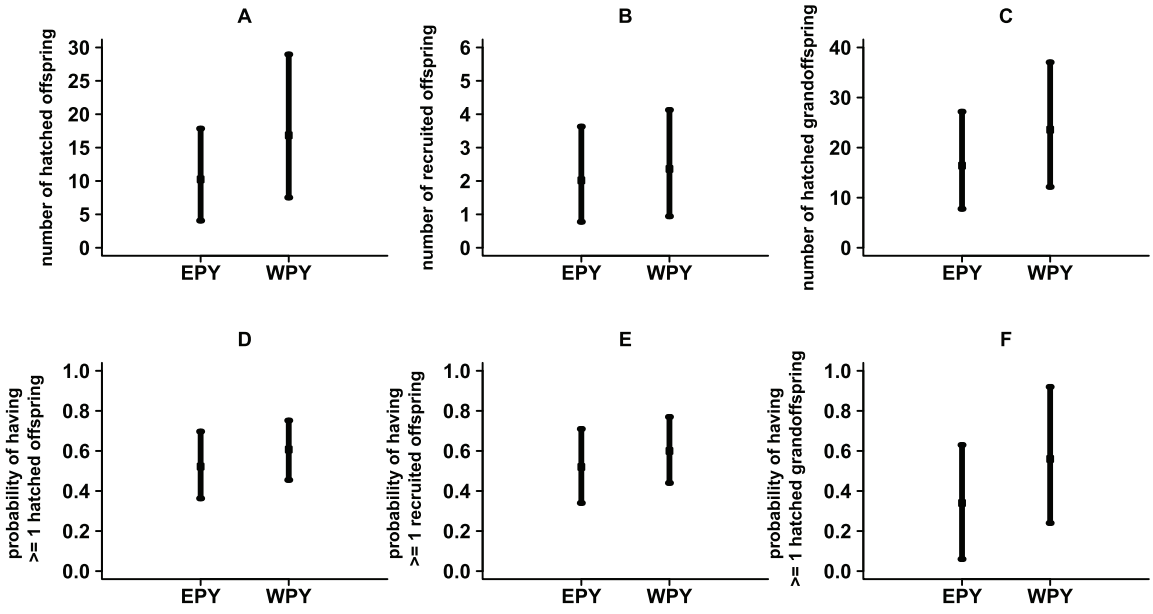

Figure 4: Back-transformed estimates (with 95% credible intervals) of the lifetime number of hatched offspring ($LRS_{hatched}$ [LRS = lifetime reproductive success]; *A*), recruited offspring ($LRS_{recruited}$; *B*), and hatched grandoffspring (LRS_{grand}; *C*); and the probability of having ≥1 hatched offspring (*D*), recruited offspring (*E*), and hatched grandoffspring (*F*) for 99 recruited extra-pair young (EPY) and extra-pair young (WPY). Estimates are from models that included a fixed effect of extra-pair status only. Estimates for *C* are from the zero-truncated Poisson process and therefore estimate LRS_{grand} given that $LRS_{grand} \geq 1$.

mean = −1.13; 95% CI, −2.45 to −0.01). Back-transformed estimates showed that EPY had an average probability of survival to hatch of 0.52 (95% CI, 0.35–0.74) compared to 0.74 (95% CI, 0.57–0.89) for WPY (a 22% absolute reduction; fig. A3).

Discussion

One empirically tractable prediction of the hypothesis that EPR partly reflects indirect selection on females is that EPY will be fitter than their WPY maternal half-siblings (Sheldon et al. 1997; Griffith et al. 2002; Arnqvist and Kirkpatrick 2005; Hasson and Stone 2011). We compared fitness between EPY and WPY maternal half-siblings from mixed paternity broods in terms of their probability of surviving to hatch and their lifetime numbers of hatched and recruited offspring and hatched grandoffspring. EPY did not differ significantly from their WPY half-siblings across almost all these metrics. Furthermore, opposite to prediction, EPY tended to have lower hatching probability and lower LRS than WPY across most life-history stages evaluated. Taken together, these results do not support the hypothesis that EPR is under positive indirect selection in female song sparrows.

Fitness of EPY versus WPY

The distributions of hatchling LRS were zero-inflated, necessitating the estimation of multiple parameters to describe the difference in fitness between EPY and WPY. On average across hatchlings of both sexes, EPY tended to have lower LRS than WPY in most analyses. Although this trend was generally not statistically significant, hatchling EPY had significantly fewer hatched offspring than hatchling WPY and estimated effect sizes were often large. Specifically, hatchling EPY had on average 40% and 30% fewer hatched offspring and grandoffspring than hatchling WPY and were 11%, 24% and 28% less likely to have any hatched offspring, recruited offspring, and hatched grandoffspring, respectively. Across EPY and WPY that survived to recruit, EPY also tended to have lower LRS than did WPY with large estimated effects. Recruited EPY had 39%, 14%, and 30% fewer hatched, recruited, and grandoffspring, respectively, and were 14%, 13%, and 39% less likely to have any of these offspring than recruited WPY. The tendency for EPY to have lower LRS than WPY, and hence for focal females to have fewer descendents via their EPY than WPY, was therefore relatively robust to the offspring stage at which LRS was measured. The only esti-

mated effect in the opposite direction was a small (5%) nonsignificant increase in the number of recruited offspring left by hatchling EPY relative to WPY.

The observation that EPY had similar numbers of recruited offspring to WPY despite having significantly fewer hatched offspring suggests that offspring of EPY may be more likely to survive to recruitment than offspring of WPY. The prediction that the offspring of EPY and WPY (rather than EPY and WPY themselves) differ in fitness has never been explicitly tested. However, since EPY had 30% fewer hatched grandoffspring than WPY, higher recruitment of offspring of EPY does not necessarily mean that EPY had higher LRS measured to the next generation. Thus, polyandrous females still tended to have fewer great grandoffspring via their EPY than via their WPY on average. Nevertheless, slight variation in conclusions drawn from analyses of different fitness measures emphasizes the value of multiple and multigenerational measures of fitness in quantifying the overall indirect benefit of mating behavior and mate choice (Brommer et al. 2004; Hunt et al. 2004).

Sex-Specific Effects

While EPY tended to have lower LRS than WPY on average, the estimated probability of having any offspring also tended to differ between male and female EPY and WPY. Female EPY hatchlings were 35%, 46%, and 52% less likely to have any hatched or recruited offspring or hatched grandoffspring than female WPY hatchlings, whereas male EPY hatchlings were 13%, 13%, and 18% more likely to have any offspring than male WPY.

Evidence of sex-specific variation in LRS with respect to extra-pair status would raise the possibility that polyandrous females gain a fitness benefit through increased reproductive success of EPY sons. Recent studies of captive insects and mammals showed that successful males sire successful sons and that polyandrous females have sons with higher fitness than monandrous females (Pai and Yan 2002; Fedorka and Mousseau 2004; Head et al. 2005; Klemme et al. 2008). Furthermore, we previously demonstrated sex-specific differential survival of EPY and WPY in song sparrows, such that female EPY were less likely to recruit and had shorter life spans than female WPY, while male EPY had similar or slightly higher survival than male WPY (Sardell et al. 2011). If such variation were evident in LRS and had an additive genetic basis, then sexually antagonistic genetic effects could shape or constrain female extra-pair reproduction (Brommer et al. 2007).

However, none of the sex-specific differences in LRS between EPY and WPY were statistically significant despite the large estimated effects, reflecting wide and overlapping CIs. Furthermore, no sex-specific difference was apparent in the number of offspring left by EPY versus WPY (rather than the probability of leaving any) or in comparisons of LRS between recruited EPY and WPY. Thus, we found no evidence of a sex-specific difference in the relative LRS of EPY versus WPY. The prediction that male EPY recruits have higher LRS than male WPY recruits, for example, because they are successful extra-pair sires (Schmoll et al. 2009), was therefore not supported in song sparrows. Indeed, in offspring of both sexes, EPY tended to be less likely than WPY to have any offspring. Any indirect fitness benefit that a polyandrous female could have accrued through EPY sons did not, therefore, outweigh the fitness cost of producing EPY daughters.

Survival to Hatch

In common with most studies that compare any measure of fitness between EPY and WPY in wild populations, our main analyses compared LRS among individuals that survived to posthatch paternity assignment. These analyses might fail to capture all fitness differences between conceived EPY and WPY if the "missing fraction" of conceived offspring that died before sampling was nonrandom with respect to extra-pair status. In our small available sample of song sparrow offspring that died before standard sampling but whose paternity could be assigned, EPY were ~30% less likely to survive relative to WPY, although this difference was only marginally statistically significant. Importantly, this tendency for EPY to be less likely to hatch than WPY mirrored the tendency for hatched and recruited EPY to have lower LRS than equivalent WPY. Overall, the available evidence regarding the relationship between offspring extra-pair status and survival to hatch therefore reinforces rather than negates the tendency for EPY to have lower subsequent fitness than WPY.

A difference in survival to hatch between EPY and WPY could greatly influence the average difference in lifetime fitness between conceived maternal half-sibling EPY and WPY. To estimate this difference we multiplied the posterior distributions for the probabilities that EPY and WPY would survive to hatch by those for the probabilities that hatchlings would leave ≥1 hatched offspring, recruited offspring, or hatched grandoffspring. These combined analyses suggested that conceived EPY tended to be less likely than conceived WPY to leave ≥1 hatched offspring (posterior modes [and 95% CIs] of 0.09 [0.04–0.14] and 0.13 [0.07–0.20], respectively), ≥1 recruited offspring (0.06 [0.03–0.11] and 0.10 [0.06–0.17], respectively) and ≥1 hatched grandoffspring (0.05 [0.02–0.10] and 0.10 [0.05–0.16], respectively). The estimates for grandoffspring indicate a twofold difference in offspring fitness in relation to extra-pair status. Furthermore, the 95% CIs around the estimates for EPY and WPY barely overlap the estimates

for WPY and EPY, respectively (fig. A4, available online). Comparing the fitness of EPY and WPY from conception, rather than the time of standard posthatch or birth paternity assignment, should therefore be a priority for future empirical studies. Adequately measuring survival to hatch may often be more feasible than measuring subsequent LRS.

Is There Indirect Selection on Female Extra-Pair Reproduction?

Our analyses show that EPY were not fitter than their maternal half-sib WPY in terms of LRS and in fact tended to be less fit. These data do not support the hypothesis that female EPR is under positive indirect selection and, if anything, suggest an indirect cost of EPR to females. Two recent meta-analyses also concluded there is no overall evidence of positive indirect selection on female EPR (Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007). Our comparisons of the fitness of EPY and WPY include multiple major life-history stages and lend substantial weight to the conclusion that EPR does not provide indirect benefits to females through increased offspring fitness (Westneat and Stewart 2003; Arnqvist and Kirkpatrick 2005; Akçay and Roughgarden 2007).

Our results are unlikely to be peculiar to song sparrows on Mandarte Island because the species regularly occurs and likely evolved in patchily distributed habitats (Arcese et al. 2002). The rates of both EPP and close inbreeding on Mandarte are also similar to those in mainland song sparrow populations (Sardell et al. 2010), and neutral genetic variation is maintained by regular immigration (Keller et al. 2001). Our study population is therefore unlikely to represent an outlier among song sparrow populations or, by extrapolation, among other philopatric species inhabiting patchy habitats.

However, strict interpretation of any phenotypic difference between maternal half-sib EPY and WPY as evidence for or against indirect selection requires that phenotypic differences between EPY and WPY reflect additive and/or nonadditive genetic effects. Maternal half-sib comparisons provide an elegant means of controlling for among-brood variation in maternal genes and environment but do not control for any environmental or parental effects on individual phenotype that covary with paternity within a brood (Sheldon et al. 1997; Griffith et al. 2002). For example, if EPY hatch earlier than WPY within a brood on average, any observed phenotypic differences between EPY and WPY may reflect environmental effects of relative hatch date rather than any intrinsic genetic difference due to paternity (Magrath et al. 2009; Ferree et al. 2010). However, recent analysis indicates that EPY also exhibit lower additive genetic breeding value for recruitment than the maternal half-sib WPY they replaced (Reid and Sardell 2012). Thus, the tendency for lower LRS in EPY than WPY has at least some additive genetic basis.

The evolution of EPR will ultimately depend on the relative magnitudes of all components of direct and indirect selection on males and females (Westneat and Stewart 2003; Arnqvist and Kirkpatrick 2005; Griffith 2007). Because our data suggest no indirect selection for female EPR through offspring fitness and in fact suggest an indirect cost, other components of selection now need to be invoked to explain the evolution and persistence of EPR. These could include direct selection on females and direct and/or indirect selection on males. These components of selection and the underlying genetic covariances among male and female EPR and fitness now need to be estimated to quantify the evolutionary forces shaping EPR (Arnqvist and Kirkpatrick 2005; Griffith 2007; Eliassen and Kokko 2008; Evans and Simmons 2008; Forstmeier et al. 2011; Reid et al. 2011*a*, 2011*b*).

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Literature Cited

Akçay, E., and J. Roughgarden. 2007. Extra-pair paternity in birds: review of the genetic benefits. Evolutionary Ecology Research 9: 855–868.

Arcese, P., M. Sogge, A. B. Marr, and M. A. Pattern. 2002. Song sparrow (*Melospiza melodia*). Pages 1–40 *in* A. Poole and F. Gill, eds. The Birds of North America: life histories for the 21st century. American Ornithologist's Union, Philadelphia.

Arnqvist, G., and M. Kirkpatrick. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. American Naturalist 165(suppl.):S26–S37.

Blomquist, G. E. 2010. Heritability of individual fitness in female macaques. Evolutionary Ecology 24:657–669.

Bouwman, K. M., R. E. Van Dijk, J. J. Wijmenga, and J. Komdeur. 2007. Older male reed buntings are more successful at gaining extrapair fertilizations. Animal Behavior 73:15–27.

Brommer, J. E., J. Merilä, and H. Kokko. 2002. Reproductive timing and individual fitness. Ecology Letters 5:802–810.

Brommer, J. E., L. Gustafsson, H. Pietiäinen, and J. Merilä. 2004.

Single-generation estimates of individual fitness as proxies for long-term genetic contribution. American Naturalist 163:505–517.

Brommer, J. E., M. Kirkpatrick, A. Qvarnström, and L. Gustafsson. 2007. The intersexual genetic correlation for lifetime fitness in the wild and its implications for sexual selection. PloS ONE 2:e744.

Charmantier, A., J. Blondel, P. Perret, and M. M. Lambrechts. 2004. Do extra-pair paternities provide genetic benefits for female blue tits *Parus caeruleus*? Journal of Avian Biology 35:524–532.

Cornell, S. J., and T. Tregenza. 2007. A new theory for the evolution of polyandry as a means of inbreeding avoidance. Proceedings of the Royal Society B: Biological Sciences 274:2873–2879.

Cornwallis, C. K., S. A. West, K. E. Davis, and A. S. Griffin. 2010. Promiscuity and the evolutionary transition to complex societies. Nature 466:969–972.

Dugdale, H. L., P. Nouvellet, L. C. Pope, T. Burke, and D. W. MacDonald. 2010. Fitness measures in selection analyses: sensitivity to the overall number of offspring produced in a lifetime. Journal of Evolutionary Biology 23:282–292.

Eliassen, S., and H. Kokko. 2008. Current analyses do not resolve whether extra-pair paternity is male or female driven. Behavioral Ecology and Sociobiology 62:1795–1804.

Evans, J. P., and L. W. Simmons. 2008. The genetic basis of traits regulating sperm competition and polyandry: can selection favour the evolution of good- and sexy-sperm? Genetica 134:5–19.

Fedorka, K. M., and T. A. Mousseau. 2004. Female mating bias results in conflicting sex-specific offspring fitness. Nature 429:65–67.

Ferree, E. D., J. Dickinson, W. Rendell, C. Stern, and S. Porter. 2010. Hatching order explains an extrapair chick advantage in western bluebirds. Behavioral Ecology 21:802–807.

Firman, R. 2011. Polyandrous females benefit by producing sons that achieve high reproductive performance in a competitive environment. Proceedings of the Royal Society B: Biological Sciences 278: 2823–2831.

Forstmeier, W., K. Martin, E. Bolund, H. Schielzeth, and B. Kempenaers. 2011. Female extrapair mating behavior can evolve via indirect selection on males. Proceedings of the National Academy of Sciences of the USA 108:10608–10613.

Gillespie, D. O. S., A. F. Russell, and V. Lummaa. 2008. When fecundity does not equal fitness: evidence of an offspring quantity versus quality trade-off in pre-industrial humans. Proceedings of the Royal Society B: Biological Sciences 275:713–722.

Grant, P. R., and B. R. Grant. 2011. Causes of lifetime fitness of Darwin's finches in a fluctuating environment. Proceedings of the National Academy of Sciences of the USA 108:674–679.

Griffith, S. C. 2007. The evolution of infidelity in socially monogamous passerines: neglected components of direct and indirect selection. American Naturalist 169:274–281.

Griffith, S. C., and S. Immler. 2009. Female infidelity and genetic compatibility in birds: the role of the genetically loaded raffle in understanding the function of extrapair paternity. Journal of Avian Biology 40:97–101.

Griffith, S. C., I. P. F. Owens, and K. A. Thuman. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Molecular Ecology 11:2195–2212.

Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1–22.

Hasson, O., and L. Stone. 2011. Why do females have so few extrapair offspring? Behavioral Ecology and Sociobiology 65:513–523.

Head, M. L., J. Hunt, M. D. Jennions, and R. Brooks. 2005. The indirect benefits of mating with attractive males outweigh the direct costs. PLoS Biology 3:289–294.

Hill, C. E., C. Akcay, E. Campbell, and M. D. Beecher. 2011. Extrapair paternity, song and genetic quality in song sparrows. Behavioral Ecology 22:73–81.

Hunt, J., L. F. Bussiere, M. D. Jennions, and R. Brooks. 2004. What is genetic quality? Trends in Ecology & Evolution 19:329–333.

Jensen, H., B.-E. Sæther, T. H. Ringsby, J. Tufto, S. C. Griffith, and H. Ellegren. 2004. Lifetime reproductive success in relation to morphology in the house sparrow *Passer domesticus*. Journal of Animal Ecology 73:599–611.

Johnsen, A., V. Andersen, C. Sunding, and J. T. Lifjeld. 2000. Female bluethroats enhance offspring immunocompetence through extrapair copulations. Nature 406:296–299.

Keller, L. F., K. J. Jeffery, P. Arcese, M. A. Beaumont, W. M. Hochachka, J. N. M. Smith, and M. W. Bruford. 2001. Immigration and the ephemerality of a natural population bottleneck: evidence from molecular markers. Proceedings of the Royal Society B: Biological Sciences 268:1387–1394.

Keller, L. F., J. M. Reid, and P. Arcese. 2008. Testing evolutionary models of senescence in a natural population: age and inbreeding effects on fitness components in song sparrows. Proceedings of the Royal Society B: Biological Sciences 275:597–604.

Kempenaers, B. 2007. Mate choice and genetic quality: a review of the heterozygosity theory. Advances in the Study of Behavior 37: 189–278.

Kempenaers, B., G. R. Verheyren, and A. A. Dhondt. 1997. Extrapair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. Behavioral Ecology 8:481–492.

Klemme, I., H. Ylönen, and J. A. Eccard. 2008. Long-term fitness benefits of polyandry in a small mammal, the bank vole *Clethrionomys glareolus*. Proceedings of the Royal Society B: Biological Sciences 275:1095–1100.

Kokko, H., R. Brooks, M. D. Jennions, and J. Morley. 2003. The evolution of mate choice and mating biases. Proceedings of the Royal Society B: Biological Sciences 270:653–664.

Lambrechts, M. M., J. Blondel, A. Caizergues, P. C. Dias, R. Pradel, and D. W. Thomas. 1999. Will estimates of lifetime recruitment of breeding offspring on small-scale study plots help us to quantify processes underlying adaptation? Oikos 86:147–151.

MacColl, A. D. C., and B. J. Hatchwell. 2004. Determinants of lifetime fitness in a cooperative breeder, the long-tailed tit *Aegithalos caudatus*. Journal of Animal Ecology 73:1137–1148.

Magrath, M. J. L., O. Vedder, M. van der Velde, and J. Komdeur. 2009. Maternal effects contribute to the superior performance of extra-pair offspring. Current Biology 19:792–797.

Pai, A., and G. Yan. 2002. Polyandry produces sexy sons at the cost of daughters in red flour beetles. Proceedings of the Royal Society B: Biological Sciences 269:361–368.

Postma, E., F. Heinrich, U. Koller, R. J. Sardell, J. M. Reid, P. Arcese, and L. F. Keller. 2011. Disentangling the effect of genes, the environment and chance on sex ratio variation in a wild bird population. Proceedings of the Royal Society B: Biological Sciences 278:2996–3002.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reid, J. M., P. Arcese, R. J. Sardell, and L. F. Keller. 2011*a*. Additive

genetic variance, heritability, and inbreeding depression in male extra-pair reproductive success. American Naturalist 177:177–187.

———. 2011*b*. Heritability of female extra-pair paternity rate in song sparrows, *Melospiza melodia*. Proceedings of the Royal Society B: Biological Sciences 278:1114–1120.

Reid, J. M., and R. J. Sardell. 2012. Indirect selection on female extra-pair reproduction? comparing the additive genetic value of maternal half-sib extra-pair and within-pair offspring. Proceedings of the Royal Society B: Biological Sciences 279:1700–1708.

Rödel, H. G., D. Von Holst, and C. Kraus. 2009. Family legacies: short- and long-term fitness consequences of early-life conditions in female European rabbits. Journal of Animal Ecology 78:789–797.

Sardell, R. J., L. F. Keller, P. Arcese, T. Bucher, and J. M. Reid. 2010. Comprehensive paternity assignment, genotype, spatial location and social status in song sparrows, *Melospiza melodia*. Molecular Ecology 19:4352–4364.

Sardell, R. J., P. Arcese, L. F. Keller, and J. M. Reid. 2011. Sex-specific differential survival of extra-pair and within-pair offspring in song sparrows (*Melospiza melodia*). Proceedings of the Royal Society B: Biological Sciences 278:3251–3259.

Schmoll, T. 2011. A review and perspective on context-dependent genetic effects of extra-pair mating in birds. Journal of Ornithology 152(suppl. 1):265–277.

Schmoll, T., F. M. Schurr, W. Winkel, J. T. Epplen, and T. Lubjuhn. 2009. Lifespan, lifetime reproductive performance and paternity loss of within-pair and extra-pair offspring in the coal tit *Periparus ater*. Proceedings of the Royal Society B: Biological Sciences 276: 337–345.

Sefc, K. M., K. Mattersdorfer, C. Sturmbauer, and S. Koblmüller. 2008. High frequency of multiple paternity in broods of a socially monogamous cichlid fish with biparental nest defence. Molecular Ecology 17:2531–2543.

Sheldon, B. C., J. Merilä, A. Qvarnström, L. Gustafsson, and H. Ellegren. 1997. Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. Proceedings of the Royal Society B: Biological Sciences 264:297–302.

Shuster, S. M. 2009. Sexual selection and mating systems. Proceedings of the National Academy of Sciences of the USA 106(suppl. 1): 10009–10016.

Simmons, L. W. 2005. The evolution of polyandry: sperm competition, sperm selection, and offspring viability. Annual Review of Ecology, Evolution, and Systematics 36:125–146.

Slatyer, R. A., B. S. Mautz, P. R. Y. Backwell, and M. D. Jennions. 2011. Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. Biological Reviews 87:1–33.

Smith, J. N. M., L. F. Keller, A. B. Marr, and P. Arcese. 2006. Conservation and biology of small populations: the song sparrows of Mandarte Island. Oxford University Press, New York.

Soulsbury, C. D. 2010. Genetic patterns of paternity and testes size in mammals. PLoS ONE 5.

Suter, S. M., M. Keiser, R. Feignoux, and D. R. Meyer. 2007. Reed bunting females increase fitness through extra-pair mating with genetically dissimilar males. Proceedings of the Royal Society B: Biological Sciences 274:2865–2871.

Taylor, S. S., R. J. Sardell, J. M. Reid, T. Bucher, N. G. Taylor, P. Arcese, and L. F. Keller. 2010. Inbreeding coefficient and heterozygosity-fitness correlations in unhatched and hatched song sparrow nestmates. Molecular Ecology 19:4454–4461.

Uller, T., and M. Olsson. 2008. Multiple paternity in reptiles: patterns and processes. Molecular Ecology 17:2566–2580.

Webster, M. S., K. A. Tarvin, E. M. Tuttle, and S. Pruett-Jones. 2007. Promiscuity drives sexual selection in a socially monogamous bird. Evolution 61:2205–2211.

Westneat, D. F., and I. R. K. Stewart. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. Annual Review of Ecology, Evolution, and Systematics 34:365–396.

Whittingham, L. A., and P. O. Dunn. 2001. Survival of extrapair and within-pair young in tree swallows. Behavioral Ecology 12:496–500.

Wilson, A. J., J. G. Pilkington, J. M. Pemberton, D. W. Coltman, A. D. J. Overall, K. A. Byrne, and L. E. B. Kruuk. 2005. Selection on mothers and offspring: whose phenotype is it and does it matter? Evolution 59:451–463.

Wilson, S., D. R. Norris, A. G. Wilson, and P. Arcese. 2007. Breeding experience and population density affect the ability of a songbird to respond to future climate variation. Proceedings of the Royal Society B: Biological Sciences 274:2539–2545.

Wolf, J. B., and M. J. Wade. 2001. On the assignment of fitness to parents and offspring: whose fitness is it and when does it matter? Journal of Evolutionary Biology 14:347–356.

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